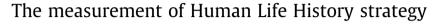
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ABSTRACT

This retrospective essay appraises J. Philippe Rushton's application of life history to understanding the covariation among human traits in light of subsequent developments in the measurement and latent structure of Human Life History, covitality, and personality. We conclude that Rushton should be recognized for having initiated a theoretically and empirically highly fertile paradigm in human individual differences research.

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1. Introduction

Differential Psychology (DP) is the study of individual differences, Behavioral Genetics (BG) is the study of their heritability, and Evolutionary Psychology (EP) is the study of how their frequencies change over generations. Although they have since drifted apart, Sir Francis Galton envisaged them as complementary facets of a unified, coherent field of study (Rushton, 1990a).

One key difference between DP and EP involves the dynamics underlying traits. DP presupposes the existence of individual differences, proceeding from there to explore their implications for a person's life, work, and social relationships. BG also takes the existence of heritable variations for granted, proceeding from there to trace their origins in our genetic material.

First and foremost, EP views traits as *strategic*, meaning differentially *selected* in phylogenies based on their consequences for survival and reproduction. *Natural Selection* represents the differential survival and reproduction of variant individuals resulting from what Darwin (1859) called their differential abilities to combat the "hostile forces of nature", meaning threats of morbidity and mortality from factors such as cold, drought, predators, parasites, and even prey. *Sexual Selection* instead entails the differential reproduction of variant individuals resulting from what Darwin (1871) androcentrically called their differential abilities to "charm the females" and "to conquer other males in battle", meaning to obtain and retain partners for sexual reproduction. Finally, *Social Selection* denotes differential success in social competition or cooperation with members of one's own species, regardless of the sex. This specific term was coined later (Nesse, 2007; West-Eberhard, 1979) because Darwin (1871) had described the process in detail but failed to label it uniquely.

Selection by Consequences provides EP with the perspective that traits may be adaptations to specific environmental contingencies (*adaptive problems*). Similarly, the genetic effects studied by BG are not taken as a given, but instead as *shaped* by selective pressures over evolutionary time.

Although few evolutionary psychologists will express these ideas bluntly, most of them are likely to agree with this representation, perhaps cautiously adding that not all traits can be presumed to represent evolved adaptations, but might instead be side-effects of adaptations or even selectively neutral. What remains controversial is at what *level* one should investigate these hypothesized adaptive functions. One currently popular view is that they should each be studied piecemeal, because the human mind is modular and each trait functions as a semi-autonomous entity that is separately shaped by its own unique selective pressures (Barkow, Cosmides, & Tooby, 1992). An alternative view is that one is well advised to examine the selective consequences of how traits, such as personality, risk taking, and health, are combined into trait clusters that may be differentially selected based on how well they do or do not work together to serve their multiple adaptive functions (Rushton, 1985a).

For the past three decades, a pioneer of this second point of view has been J. Philippe Rushton, who was among the first to see how Life History (LH) theory (MacArthur & Wilson, 1967; Pianka, 1970) could be productively applied to make sense of the otherwise seemingly incomprehensible clustering of traits that we observe. LH theory describes the ways organisms allocate resources among different components of fitness, given the environmental constraints under which they survive and reproduce. LH strategies range from those based on maximizing reproductive



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outcomes as a buffer against environmental unpredictability, to those based on maximizing longevity and parenting, so as to enhance the quality and competitiveness of organisms living in stable environments (Ellis, Figueredo, Brumbach, & Schlomer, 2009). LH strategies have traditionally been characterized as *r*-selected and *K*-selected, representing opposite poles of a continuum. The former comprises species exhibiting very fast life histories (e.g., rabbits), with *r* denoting the maximum population reproductive rate of that species. The latter encompasses species exhibiting very slow life histories (e.g., elephants), which saturate their environment to carrying capacity (K). For example, a high mating effort strategy represents a fast life history owing to the tendency for enhanced reproduction to be associated with more rapid maturation and to come at the expense of longevity, whereas the high somatic effort and *parental effort* strategy represents a *slow* life history, owing to its theoretical and empirical associations with slower ontogenic development and enhanced longevity (Figueredo, Vásquez, Brumbach, & Schneider, 2004; Figueredo et al., 2005).

Rushton (1985a) made a series of innovative predictions concerning the relationship between individual differences and LH strategy, a substantial number of which have been empirically validated by subsequent work. Rushton's original (1985a) paper initiated an alternative research tradition in LH theory (See: Rushton, 1985b, 1985c, 1987a, 1987b, 1988a, 1988b, 1990a, 1990b, 1991, 1992, 2000, 2004; Bogaert & Rushton, 1989; Figueredo & Rushton, 2009; Rushton & Ankney, 1993; Rushton & Bogaert, 1988; Rushton & Templer, 2009; Rushton & Whitney, 2002; Templer, 2008; Templer & Rushton, 2011). This bold idea proposed that hierarchically organized and heritable individual differences variables such as personality and intelligence share a common source of variance stemming from life history, which acts to co-ordinate tradeoffs among traits. He proposed that heritable variations in LH strategy are not only at the root of human individual differences but are also at the root of ethnic/racial and socioeconomic status differences along the same parameters.

Perhaps the most significant of these claims is that LH strategy can be measured as an individual differences variable in its own right. Bogaert and Rushton (1989) were the first to explore this possibility with their life history questionnaire, among whose 18 constituent measures a latent LH factor was identified. Bogaert and Rushton included items directly measuring ecological factors such as density, dispersion and competition, in addition to attitudinal and physiological factors. This approach integrated with earlier density-dependent conceptualizations of LH evolution (Pianka, 1970), as these are measures of individual differences in ecological preferences.

Whereas many of us originally trained in the biological sciences were quite conversant in LH theory before encountering the work of Rushton, we simply did not envision all the implications he derived for human differential psychology. For example Rushton (1985a) derived the following prediction: "An exciting if openended possibility is that one basic dimension -K – underlies much of the field of personality" (p. 445). Consistent with this theoretical expectation, a General Factor of Personality (GFP) has now been extracted from over 24 different personality inventories (Rushton & Irwing, 2011) and is predicted to exist in others (Woodley & Bell, 2011). Rushton (1985a) also predicted that health outcomes (such as disease resistance and longevity) might share a common variance with LH strategy, owing to the organismic quality versus quantity tradeoff implicit in LH theory. Consistent with this prediction is the finding of a latent Covitality factor in biomedical and subjective well-being measures (Weiss, King, & Enns, 2002). Contemporary measures of LH strategy, not based on density-dependent selection, have been found to correlate so strongly with both the GFP and this Covitality Factor that a higher-order factor has been extracted explaining the preponderance of the covariance among the three lower-order factors (e.g., Figueredo, Vásquez, Brumbach, & Schneider, 2006; Figueredo, Vásquez, Brumbach, & Schneider, 2007; Figueredo et al., 2004; Figueredo et al., 2005). The existence of this higher-order LH factor validates some very important predictions made by Rushton (1985a), in that it has been found to exhibit a modestly high heritability ($h^2 \sim .65$; Figueredo et al., 2004; Figueredo et al., 2005), which corroborates Rushton's prediction that human LH is a biologically prepared disposition rather than simply a product of socialization, as previous researchers had proposed. The modestly high heritability of this higher-order LH factor further accords with Rushton's utilization of the standard assumption of BG, namely that very few traits are purely heritable and that all individual difference traits are also modestly environmentally plastic. Indeed, consistent with this position, much recent research indicates that humans are able to adaptively calibrate their life histories in response to perceptions of environmental stability during key phases of development (Del Giudice & Belsky, 2011; Ellis et al., 2009).

Prior to the work of Rushton, explaining why there exists so much observable covariation among socially problematic behaviors (e.g., timing of intercourse, alcohol/drug usage, etc.) had perplexed social scientists. Most explanations offered were *proximate*, meaning immediately causal or developmental mechanisms for these life outcomes, ignoring any *ultimate explanations* regarding the possible adaptive significance of this covariation (Cabeza de Baca, Figueredo, & Ellis, in press). The prevailing proximate explanation was that *social privilege*, meaning the institutional advantages a family possessed (e.g., due to interethnic social dominance, higher income, higher social class, etc.) could account for behavioral variation both between and within groups (Figueredo et al., 2007).

In the 1960s and 1970s, however, the sociobiology movement urged social scientists to incorporate ultimate or evolutionary explanations in the study of human behavior (e.g., Dawkins, 1976; Hamilton, 1964; Trivers, 1972; Williams, 1966; Wilson, 1975), proposing that the social sciences could be unified into a broader biological sciences framework conducive to the generation of novel distal-level hypotheses (Cabeza de Baca et al., in press: King & Cabeza de Baca, 2011). Unfortunately, this synthesis was met with resistance from the social sciences, citing melioristic reasons, such as the perpetuation of inequity and the justification for deprived conditions among disadvantaged groups (Charlesworth, 1992; King & Cabeza de Baca, 2011). Despite resistances, social science started taking notice of the new evolutionary framework that sociobiology evoked. By the late 1970s and 1980s, nuanced approaches of sociobiology began to emerge. Specifically, researchers began to examine physiological, personality and other individual differences contextually, noting that, beyond human universals, adaptations were context-specific. Weinrich (1977) examined the variation between racial and socioeconomic classes differences concerning sexual behavior and patterns of pair bonding - citing that resource unpredictability, conceptualized as family income, could differentially impact sexual decision-making. By 1983, Reynolds and Tanner (1983) began incorporating context via religious practices and societal culture, systematically reviewing differences in conception, adolescence, and marriage, among others. Also, in 1983, a workshop discussing the merits of LH theory on human research was convened by representatives from anthropology, psychology, and biology (Weigel & Blurton-Jones, 1983).

Aside from these early precursors, we maintain that it was the work of Rushton that gave direction to nearly all that followed. Unfortunately, his work on the psychometrics of LH strategy was overshadowed by the controversy surrounding his prediction of race differences in LH strategy as adaptations to ancestral ecological conditions in the different regions of the world.

2. The psychometrics of Human Life History

Contemporary LH theory suggests that there might be a number of factors, independent of density-dependent selection, that give rise to differences in life history speed. Contemporary measures of human LH strategy incorporate these newer perspectives while elaborating the *nomological net* first established by Rushton (1985a) for the specific implications of LH strategy in our species.

2.1. Cognitive and behavioral indicators of slow life history strategy

Using an undergraduate student sample, Figueredo et al. (2005) estimated a slow LH factor that loaded positively and significantly on Attachment to and Investment from their Biological Father and Adult Romantic Partner Attachment, and loaded negatively and significantly on Attachment to and Investment from any "Other" Father Figure, the Mating Effort Scale, Machiavellianism Scale, and Risk Taking Questionnaire. Using an ethnically homogeneous sample of Mexican, non-student adults with children of their own, Tal, Hill, Figueredo, Frías-Armenta, and Corral-Verdugo (2006) estimated a slow LH factor that loaded positively and significantly on Long-Term Planning, Father's Parental Investment, Mother's Parental Investment, Parental Investment Towards Children, Social Contact and Support from Family and from Friends, Responsibility and Support for Kin and for Non-Kin.

The 20 cognitive and behavioral scales identified from within the National Survey for Midlife Development in the US (MIDUS; Brim et al., 2000) data by Figueredo et al. (2007) as theoreticallypredicted convergent indicators of a latent variable (K) representing slow LH strategy, measured the following psychosocial traits: Agency, Advice Seeking, Foresight/Anticipation, Insight Into Past, Primary Control/Persistence, Flexible/Positive Reappraisal, Self-Directedness/Planning, Financial Status, Health Control. Mother and Father Relationship Quality, Marital Relationship Quality, Children Relationship Quality, Family and Friends Social Support, Altruism Towards Kin and Non-Kin. Close Relationship Ouality. Communitarian Beliefs, and Religiosity. All of these scales had common factor loadings from the slow LH factor ranging from \sim .30 to \sim .60. In the MIDUS twins (Figueredo et al., 2004), all of these psychosocial traits had genetic factor loadings from the slow LH factor ranging from \sim .50 to \sim 1.00, except for Agency and Health Control, which had no significant genetic covariance.

Using a composite college student sample, Sefcek and Figueredo (2010) subsequently constructed a slow LH factor loading positively and significantly on the Mini-K (Figueredo et al., 2006) (A 20-item short form of the 199-item, Arizona Life History Battery or *ALHB*; Figueredo, 2007), Mother and Father Parental Investment, Family Social Support, Friends Social Support, Romantic Partner Attachment, and General Altruism. Gladden, Figueredo, and Jacobs (2008) obtained similar findings with an independent student sample, estimating a slow LH factor loading positively and significantly on the Mini-K Short Form, Insight, Planning, and Control, Mother and Father Parental Investment, Family Social Support, Romantic Partner Attachment, and General Altruism, and Religiosity. This particular set of cognitive and behavioral indicators constituted the *ALHB* (Figueredo, 2007), which has been used in a variety of subsequent studies.

With respect to criterion-related validity, a variety of investigators have found that using either this entire set or some restricted subset of cognitive and behavioral indicators, one can: (1) positively and significantly predict Executive Functions, Trait Emotional Intelligence, Mate Value Inventory, Mate Value Scale, Rosenberg Self Esteem Scale, Self-Adjective Checklist, Social Economic Exchange Scale, Collective Self Esteem Scale, Positive Assortative Mating, Female Physical Height, Long-Term Mating Sociosexual Orientation, Moral Intuitions, In-Group Loyalty, as well as Secure Attachment, Supportive Communication, and Long-Term Satisfaction in Romantic Relationships, both cross-sectionally and longitudinally; and (2) negatively and significantly predict the Mating Effort Scale, Short-Term Mating Sociosexual Orientation, Escalated Mate Retention Tactics, Affective and Punitive Responses to Sexual or Emotional Infidelity, Intimate Partner Violence, Interpersonal Aggression, Female Intrasexual Competitiveness, Disordered Eating Behavior, Negative Ethnocentrism, Negative Androcentrism, Levenson's Primary Psychopathy Scale, Levenson's Secondary Psychopathy Scale, Machiavellianism Scale, Buss-Perry Aggression Questionnaire, Proactive-Reactive Aggression Questionnaire, and General Social Deviance (e.g., Buunk, Pollet, Klavina, Figueredo, & Dijkstra, 2009; Figueredo, Andrzejczak, Jones, Smith-Castro, & Montero-Rojas, 2011: Figueredo, Gladden, & Beck, 2011: Figueredo, Gladden, & Hohman, 2011: Figueredo & Wolf, 2009: Gladden, Sisco, & Figueredo, 2008: Gladden, Figueredo, & Snyder, 2010; Jones, Figueredo, Dickey, & Jacobs, 2007; Kirsner, Figueredo, & Jacobs, 2009; Olderbak & Figueredo, 2009; Olderbak & Figueredo, 2010; Salmon, Figueredo, & Woodburn, 2009; Wenner, Figueredo, Rushton, & Jacobs, 2007).

2.2. Slow life history and the general factor of personality

As previously noted, the General Factor of Personality (GFP) predicted by Rushton has now been extracted from over 24 different personality inventories (Rushton & Irwing, 2011), is robust to meta-analysis (van der Linden, Scholte, Cillessen, te Nijenhuis, & Segers, 2010), and exhibits a heritability of around .50 (Rushton, Bons, & Hur, 2008). Like the *g*-factor in intelligence research, the GFP is believed to exist at the apex of a hierarchy of personality traits, with Digman (1997) and DeYoung et al.'s (2002) Big Two traits (Stability or Alpha; and Plasticity or Beta) occupying the next level and Costa and McCrae's (1992) Big Five (Openness, Conscientiousness, Extraversion, Agreeableness and Neuroticism) occupying the next level, and so on (Rushton & Irwing, 2011). The GFP also exhibits modest criterion related validity (van der Linden, te Nijenhuis, & Bakker, 2010; van der Linden, Bakker, & Serlie, 2011).

2.3. Slow life history and covitality

Because slow LH Strategists, by definition, allocate more bioenergetic and material resources to somatic effort, meaning growth and self-maintenance, we expect them to generally manifest better health and life expectancy. These individuals expend more effort on their personal condition and also receive more parental effort and nepotistic effort from family members (who share genes biasing development towards slow LH strategy), as well as more mutualistic and reciprocal altruism from non-relatives, including romantic partners, with whom they are more likely to develop long-term cooperative relationships.

This theoretical prediction has been tested and confirmed in a number of studies. Using data from *MIDUS*, Figueredo et al. (2004) related a latent variable representing slow LH strategy (K), composed of 20 convergent indicator scales, to a general factor representing a state of overall physical and mental health (*Covitality*). The latter construct loaded positively on Subjective Well-Being, Positive Affect, and General Health, and loaded negatively on Negative Affect and Medical Symptoms.

The *MIDUS* data were collected from telephone interviews and two follow-up mail surveys given to a nationally representative sample in 1995–1996, sampled only 25–74 year-old English speakers in the US, and also contained a genetically informative sample of MZ and DZ twins.

In the subsample of singletons, the phenotypic correlation between the slow LH and Covitality factors was .50. In the subsample of twins, the phenotypic correlation between the slow LH and Covitality factors was .54, and the genetic correlation between the slow LH and Covitality factors was .69. All these correlations were highly statistically significant. Figueredo and Rushton (2009) followed up with more sophisticated biometric structural equations modeling and found that a higher-order LH factor termed Super-K loaded on slow LH, Personality and on this same Covitality factor (.63). This common factor variance was decomposed into 17% additive genetic variance, 8% attributable to shared environmental influences among twins raised together, and 36% attributable to unmeasured environmental influences that were not shared among them. The other indicators of the Super-K factor manifested no significant variance component attributable to shared environmental influences. Unlike these other LH indicators, however, the Covitality factor showed no significant non-additive genetic variance component attributable to "dominance" effects. meaning multiplicative gene-gene interactions.

Using a composite student sample, Sefcek and Figueredo (2010) subsequently constructed another Covitality factor, which loaded .31 on the slow LH factor. This Covitality factor loaded positively and significantly on the General health scale, the MOS SF-36 Short Form Health Survey, the Subjective Well-Being Scale, but negatively and significantly on the Medical Symptoms Scale, the Hop-kins Anxiety Index, the Hopkins Depression Index, and the Beck Depression Inventory.

3. Conclusions

The application of life history theory to DP has developed into a sophisticated and nuanced analysis that has gained widespread utilization in diverse research ranging from pubertal timing (Ellis, 2004), to parenting (Cabeza de Baca et al., in press; Sotomayor-Peterson, Cabeza de Baca, Figueredo, & Smith-Castro, in press), to religiosity (Gladden, Welch, Figueredo, & Jacobs, 2009). Widespread application of LH theory would not have been possible without researchers within their respective fields reformatting their existing measures and conceptualizing their hypotheses to incorporate LH theory. Nonetheless, we expect more progress will be made toward the measurement of LH.

It is evident that Rushton's application of LH theory to understanding individual and group differences constitutes a significant and novel contribution to explaining the observed covariation among human behaviors. Rushton made many bold predictions and most have been supported to varying degrees by the preponderance of research that followed in his scientific wake. Rushton's work must further be praised for its willingness to engage with controversy. While not accorded the fullest general recognition that his work deserves in this current day and age, ultimately posterity will be the judge of the value of his work.

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